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work, "Das Antlitz der Erde," has fully demonstrated the fallacy of this theory. If Dr. Alfred Russel Wallace[26] would have studied this work and those of W. T. Blanford, O. Feistmantel, W. Waagen, Melchior Neumayer, and others, he could not have accepted the theory of the permanence of the great oceanic basins, which he still defends in 1892, quoting the late Prof. Dana, Mr. Darwin, Sir Archibald Geikie, Dr. John Murray, Rev. O. Fisher and himself as authorities, not mentioning any of the names just given.

We know now that there existed a *Lemuria* or *Gondwana Land*, an *Antarctic Continent*,[27] which extended to India, South Africa, South America, and that the Pacific Ocean has not been an ocean since palæozoic or archæan times, but is probably even of recent (Tertiary) date.

In order to reach correct conclusions about these often very complicated questions, it is necessary to use all the data offered by modern geographical and palæontological distribution of fauna and of flora geology.

(*To be Continued.*)

ON THE AFFINITIES OF TARSIUS: A CONTRIBUTION TO THE PHYLOGENY OF THE PRIMATES.

BY CHARLES EARLE.

(*Continued from page 575.*)

The female reproductive system of the Lemurs recalls that of the Anthropoids. It is interesting to note that in *Lemur Propithecus* and *Indris* only one young is produced at a birth; whether this number of young is typical of the whole suborder of *Lemuroidea* I am unable to discover. The form of the uterus exhibits considerable variation in the Lemurs. Milne-Edwards says: "L'Uterus des Indrisines a la forme d'une poche median dont le fond est bicorne les deux lobes ainsi constitués sont tres peu saillants chez les Propithiques et les Avahis, ils le sont davantage chez l'Indris." In *Propithecus* especially, the cornua are extremely reduced, and externally the uterus has the appearance of the uterus simplex of the Anthropoids. In the gravid uterus, owing to the extremely small size of the cornua, the single fœtus occupies one horn and all the body of the uterus; in *Lemur* the non-gravid cornua is occupied as shown by Turner by a prolongation of the chorion. It is not difficult to imagine the derivation of the uterus of the Apes from the condition found in the higher Lemurs, further constriction of the fallopian tubes of *Propithecus* and obliteration of the slight septum dividing the rudimentary cornua of this genus would produce the pure type of uterus simplex found in the Apes.

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[26] Wallace, Dr. A. Russel. The Permanence of the Great Oceanic Basins. Nat. Science, Vol. I, No. 6, August, 1892, p. 418–426; and "Island Life," second ed., 1892.

[27] Seward, A. C. The Glossopteris Flora. Science Progress, New Series, Vol. I, No. 2, January, 1897, p. 178–201. (This paper gives the Bibliography relating to the Anarctic continent.)

I will now pass on to consider the palæontological history of the Primates and the conclusion which may be drawn from it. Prof. Hubrecht claims that throughout the whole Tertiary period the Lemurs and Apes were perfectly distinct, and, moreover, he concludes that we must go as far back as the Mesozoic to find the two stem forms of these suborders. I hold there is absolutely no palæontological evidence to support this deduction, and all our knowledge of the fossil Primates show that the Apes have arisen later than the Lemurs. Prof. Hubrecht, following Ameghino, refers the Santa Cruz formation, in which *Homunculus* occurs, to the Eocene. All palæontologists now admit that the Santa Cruz beds are of much later date than the Eocene, and it appears probable that they are not earlier than the Lower Miocene. If there is anything in the biological law that less specialized forms originate earlier than the more modernized types, it is surely applicable to the Primates where every one must acknowledge that an Ape is a much more highly differentiated organism than a Lemur.

I will not consider the so-called Primates from the lowermost Eocene, Puerco. We know little about these forms, but, as far as our knowledge goes, such genera as *Indrodon* and

Mixodectes appear to be related to the Lemurs, but in the case of *Indrodon* the shape of the external cusps of the superior molars are not at all *lemurine*, and resemble more those of the *Cheiroptera.*

The Wasatch genus, *Anaptomorphus,* has been placed by Hubrecht with Tarsius, among the Apes and for what reason? It certainly has only one Anthropoid character, the presence of an internal lobe to the third upper premolar. If *Anaptomorphus* is an Ape, then I claim that this is absolute evidence that the Apes have come from the Lemurs, for *Anaptomorphus* is in all of its characters a Lemur closely related to *Tarsius.* However, *Anaptomorphus* is an important type in connection with the phylogeny of some of the Anthropoids, and may have given origin to the American Monkeys, these latter having arisen independently from the Old World Apes. Numerous peculiarities in the structure of the *Cebidæ* as compared with the *Cercopithecidæ* support this view. Excepting *Anaptomorphus* it appears probable that none of American fossil lemurines can be considered as ancestral to either the recent Lemurs or Apes.

In the Oligocene of France the primitive Lemurs were very abundant, and they were represented by numerous genera other than the well-known *Adapis* and *Microchoerus.* Consequently, as far as we know, the recent Lemurs must have been derived from some of the genera now found as fossils in Northern Europe. Mr. Lydekker is of the opinion that Apes occur in the Oligocene of France, but I have not been able to find any evidence for this view, as most of the supposed Apes from the Phosphorites have been shown to be Suillines. The structure of the upper molars of *Adapis* is very similar to that of recent Lemurs, the external lobes being lenticular in section as in recent forms, the protocone is placed well forward and the hypocone is more primitive than in many of the *Lemurinæ.* As far as I have examined, all recent genera of the subfamily *Lemurinæ* have tritubercular superior molars with varying development of the supplementary internal cusps. In the *Indrisinæ* the molars are truly quadritubercular and the internal cusps are nearly selenoid in structure. It is strange that among American Monkeys, *Mycetes* has a type of superior molar which closely resembles that of the *Indrisinæ,* whereas, in the other *Cebidæ,* the upper back teeth are transitional in structure, between the tri- and quadritubercular types, and the cusps are bunoid. The molar pattern of recent Lemurs and Old World Apes is fundamentally different, but they may be brought into closer relations by means of the primitive structure of the molars of *Tarsius* or *Anaptomorphus.* If *Tarsius* stands near the common ancestor of both Apes and Lemurs, then we must suppose that the teeth of the two phyla of recent Primates have increased in complexity during geological time. Nevertheless, in the Anthropoid Apes the molar pattern shows plainly a process of degeneration from a higher type, more like that found in the *Cercopithecidæ.*

Until recently no known Primate, fossil or recent, possessed a closed orbit as in the Apes and proclivous incisors and caniniform first lower premolar as in the Lemurs. This combination of characters is found in the Malagasy fossil lately described by Forsyth Major under the name of *Nesopithecus.* The skull, as far as known in *Nesopithecus,* is broad and short like that of the Apes, and as in the latter group the lachrymal foramen is within the orbit. Again, the structure of the true molars is exactly like that of the Anthropoids. On the other hand the form of the premolars is more like that of the Lemurs, and, as far as I can learn from Major's figures, all the upper premolars have small internal lobes. The incisors of *Nesopithecus* are not preserved, but from the oblique position of their alveolii Major concludes that these teeth must have been horizontal as in the living Lemurs. Moreover, as in the latter group, the first lower premolar functions as a canine. The collection of characters occurring in *Nesopithecus* completely breaks down the differential characters of the skeleton which is usually given as separating the Lemurs from the Apes. Either these two groups should be united, or *Nesopithecus* must be placed in a new suborder of the Primates. It remains now to consider whether *Nesopithecus* clears up the problem of the relation of the Lemurs to the Apes. Lydekker is of the opinion that *Nesopithecus* is a form closely related to the stem type which gave origin to both Lemurs and Apes. For my part, I do not think that this explanation is probable, and for the reason that no primitive ancestor of the Primates would have had a closed orbit and proclivous lower incisors. At the time the Apes and Lemurs diverged from a common stock, this stem form would have had characters more like those of the *Adapis*, and not until very late, geologically speaking, were the peculiar incisors of the Lemurs developed. Primates with closed orbits do not appear until the Middle Miocene. We are then forced to the conclusion that one set of characters of *Nesopithecus* is due to convergence. As *Nesopithecus* has so many peculiar characters only found in the Anthropoids, including the structure of the true molars, I conclude with Major that *Nesopithecus* is really an Anthropoid whose anterior dentition through convergence has come to resemble that of the Lemurs. Lastly I do hold that the discovery of *Nesopithecus* demonstrates that Apes and Lemurs are genetically related.

The characters of the skeleton of *Tarsius* are nearly all those of the Lemurs; the extreme specialization of the pes of *Tarsius* is clearly a lemurine character, and we can observe how this elongation of the tarsus is produced. In *Lepidolemur* the elongation of the calcaneum and navicular commences, the extension of these bones is carried still further in *Cheirogaleus*, and reaches its culmination in *Tarsius*. Of course this is not a phyletic series, and I merely mention it to show how the elongation of the tarsus in *Tarsius* is developed, and from a more normal condition found in the typical Lemurs. *Tarsius* differs from most of the Lemuroidea in not having the fourth digit of the manus longer than the others, the extension of this digit attains its greatest development in the most specialized group of the Lemurs, the *Indrisinæ*. The Indrisines are clearly the most highly differentiated division of the Lemurs; this is shown in their more highly developed brains, reduction in the length of the facial as compared to the cranial axis of the skull, the pseudo-selenoid superior molars, and lastly the great length of the posterior limbs in contrast with the anterior members. In this connection it is interesting to note that the *Indrisines* are diurnal in their habits like most Apes, and that in *Indris* the caudal appendage is much reduced in size.

Forbes pointed out the important fact that the structure of the orbit in the Old and New World Apes differs; in most of the *Cebidæ* there is a large articulation between the malar and parietal, the broad plate-like alisphenoid is limited to the inferior portion. In the *Cercopithecidæ* the alisphenoid is narrow and prolonged above to the frontal, so as to separate the malar-parietal contact. In the structure of its orbis *Tarsius* more resembles the Old World Apes, for the alisphenoid articulates with both malar and frontal as in the *Cercopithecidæ.* The structure of the skull of *Tarsius* is of importance as showing how the closure of the orbit of the Apes is brought about. It is evident that the relations of the orbital bones found in the *Cebidæ* is the primitive one, the broad and inferiorly placed alisphenoid is characteristic of the lower orders of Mammals, as the Rodents and Carniverous Marsupials. Coincident with the increase in breadth of the frontal lobes of the cerebrum of *Tarsius* as compared to other Lemurs, has taken place a reduction of the facial portion of the skull, and with it the near approach of the lachrymal foramen to the orbital border. *Nesopithecus* represents another step in the evolution of the skull of the Apes from that of the Lemurs, as in this form the facial axis is still more reduced, and at the same time the lachrymal foramen has been taken within the orbit. In *Nesopithecus* the orbits are directed forwards as in the Apes, and Forsyth Major concludes from the broken condition of the posterior orbital wall, that this genus had a completely closed orbit. The skull of *Tarsius* represents a stage in the evolution of the Primate cranium exactly intermediate between that of the Apes and Lemurs. Among the typical Lemurs the general form of the cranium in the *Indrisinæ* is closely similar to that of *Tarsius.*

Although the structure of the molars in *Tarsius* is very primitive, and may represent the ancestral pattern from which that of the Lemurs and Apes has been derived, this cannot be claimed for the anterior part of the dentition. The reduction in size of the canines in *Tarsius* and the enlarged upper median incisors is certainly a case of specialization. We see this same change in the *Insectivora,* and Flower concludes: "The strongly marked distinction of the canines from the incisors and anterior premolars in the Mesozoic and most of the Tertiary Mammals (excepting some Ungulates) points, however, very decidedly to the conclusion that the want of definition between these teeth in many of the modern *Insectivora* is an acquired feature." I quote this passage from Flower and Lydekker, because an important paper by Leche has lately appeared in which he claims that the milk teeth represent an earlier development phase than the permanent teeth. He arrives at this generalization from a study of the milk dentition of the Lemurs, including *Tarsius*. Leche finds, for example, that in the anterior milk dentition of *Adapis magnus* the milk canines are much reduced in size, and more resemble the form of the premolars, and he also points out that the deciduous dentition of this species of *Adapis* very closely resembles the permanent condition of *Adapis parisiensis*. Leche concludes, therefore, that *A. parisiensis* represents the most primitive and ancestral form of *Adapis* known, and that the Ape-like form of the incisors and canines of *A. magnus* is a secondary condition derived from that of *Adapis parisiensis*. I feel confident that palæontologists will not accept this dictum in regard to the significance of the milk dentition as expounded by Leche. I should like to notice one point that seems to contradict this general law as deduced by Leche. In *Tarsius*, for example, Leche's figures plainly show that the upper milk canine is larger than either of the milk incisors or the anterior premolars. If the structure of the anterior milk teeth is to be our guide in determining the evolution of the Lemurs, then *Tarsius* has come from a type which had large canines and in which these teeth were erect and of greater size than either the incisors or premolars. This conclusion corresponds better with the palæontological record.

One of the best examples of extreme specialization and reduction in the size of the canines is the case of the *Anoplotheridæ*, an extinct family of Artiodactyle Ungulates. In this group the dentition is closed and the canines are of the same size and structure as the anterior premolars. I am sure that no palæontologists will claim that the dentition of the *Anoplotheridæ* is primitive, as the whole structure of this family denotes that it is an exceedingly specialized group. I have endeavored to show elsewhere that *Tapirulus* is probably genetically related to the Anoplotheroids, and in this genus the canines are fully developed. As far as I can learn it is a general character of the milk dentition that the milk canines are weakly developed and much smaller than their permanent successors. It appears more likely that the milk dentition represents a special adaption during the time that the young animal is nourished by the mammary glands of the mother, and that the detailed structure of the milk teeth do not accurately recapitulate the ancestral stages in the evolution of the race. However, in regard to the number of the milk teeth, that is another question, for we know that in many types which in the adult condition the permanent teeth are greatly reduced in number, whereas in the milk series the lost teeth appear. Among Lemurs *Cheiromys* is a good example in the reduction of the teeth, where the milk dentition is more normal in regard to the number of teeth than the permanent dentition, and plainly shows that *Cheiromys* has been derived from some more generalized type of Lemur, which had the normal number of incisors and premolars.

In conclusion, the two principal objections in claiming that the Lemurs are genetically related to the Apes are, first, in the apparently great difference in their placentation, and secondly, in the wide divergence in the structure of their dentition. In regard to the evolution of the placenta, Dr. Minot remarks that our conceptions are still very obscure. The views of Balfour which I have lately quoted[2] as to placental evolution in the Primates are clearly untenable, for the reason, as I have emphasized before, that in the Apes the allantois is rudimentary and the placenta arises in the chorion. It is most important for the position which I maintain in regard to the relations of the Lemurs to the Apes, to notice that in the early stages of the development of the placenta in the Anthropoids that this organ is completely diffuse and there is no decidua. This stage is comparable to the diffuse placentation of the Lemurs. On any theory of the evolution of the placenta in the Primates we must first commence with the non-deciduate diffuse condition as found in Man, the later restriction of the placental area brings about complications in the relations of the maternal to the fœtal surfaces, resulting in the formation of a decidua. Hubrecht himself admits that *Tarsius* is very specialized in not exhibiting in its early stages the diffuse condition of the placenta found in the Anthropoids. It seems to me that it is a most difficult problem to attempt to derive the type of placentation of the Apes from that of *Erinaceus.* In the latter genus the placenta is derived from the allantois, which is a large free organ before it unites with the chorion. Then, again, in *Erinaceus* there is no early stage where the mesoblast lines the whole blastocyst as in *Tarsius,* and a portion of which membrane takes a share in the formation of the placental anlage. The *Insectivora,* however primitive they are in many respects, are greatly specialized in their dentition and placentation.

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[2] See Natural Science, May 1897.

Huxley remarks: "If *Gymnura* possessed a diffuse placentation, it would be an excellent representative of an undifferentiated Eutherian." Again, he says: "The derivation of all Eutheria from animals which, except for their placentation, would be insectiverous, is a simple deduction from the law of evolution." That some *Insectivora* are highly degenerate in their cranial and dental structures, I think must be admitted. I refer particularly to *Hemicentetes,* whose supposed primitive type of molars is clearly a case of degeneration from the more normal form of tooth occurring in *Centetes.*

Until it is disproved by further investigations on the early stages of Lemurs, I think it is most plausible to assume that the diffuse placenta of the Lemuroidea is one of the ancestral stages in the evolution of the Anthropoid placentation, and in the case of Man this diffuse non-deciduate stage is recapitulated in the ontogeny of *Homo.*

As far as the palæontological evidence goes it is decidedly in favor of the view that Apes and Lemurs are closely related. Beginning with the earliest known Lemur, *Anaptomorphus,* this genus shows tendencies towards the Anthropoids, and when we pass up into the Oligocene of the Old World, *Adapis* is a decidedly mixed type, and probably not far from the common stem form, which gave origin to both suborders of the Primates.

In regard to *Tarsius*, it is evidently a type nearly between the Lemurs and Apes, but with many essential characters belonging to the former group. Some of its Anthropoid characters are nascent, so to speak; they are just developing, and, as in the case of the orbit of *Tarsius*, it is not yet fully differentiated into the higher type of the true Anthropoids. It appears most likely that the group of fossil Lemurs with reduced canines and enlarged incisors, *Mixodectes*, *Microchœrus*, were not in the line leading to the Lemurs proper, but may have been related to *Cheiromys*. These genera in their turn arose out of a generalized insectivorous-like type with a normal dentition, which was also the ancestral form of the true Lemurs. The Anthropoids diverged from a lemurine stock probably not earlier than the Upper Eocene. This deduction is supported by the fact that the first Lemurs to appear are insectivorous in their affinities; later, in the Upper Eocene, Lemurs are found with quite Ape-like skulls and dentition, and, moreover, not until the Miocene do true Anthropoids appear.

I shall conclude this paper with a quotation from a Memoir of Sir Wm. Turner's, whose extensive investigations on the placentation of Mammals are well known to all morphologists: "In the case of the Lemurs it will, I think, be considered by most zoologists that the characters of the teeth, the general configuration of the skeleton, the unguiculate digits, the hand-like form of the distal part of the extremities, the presence of a calcarine fissure in the cerebrum and the pectoral position of at least two of the mammæ, are characters which indicate that the Lemurs have much closer affinity with those mammalian orders with which it has been customary to associate them, than with the Perissodactyla, Suina and Cetacea. Collectively, these characters ought, I think, to be regarded as more valuable indications of structural affinity than should the presence in the Lemurs of a non-deciduate diffused placenta with a large allantois be regarded as indications of structural dissimilarity from the Apes and Insectivora, though the placenta in the latter is deciduate and discoid and the allantois aborted."